STUDIES ON THE PHLOEM OF THE DICOTYLEDONS[1]

I. PHLOEM OF THE JUGLANDACEAE

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(WITH PLATE XIII)

During the past year the writer has studied the phloem of *Juglans nigra*, *Juglans cinerea*, *Carya ovata* (hickory nut), *Carya alba* (mocker nut), *Carya glabra* (pig nut), and *Pterocarya caucasica* (Caucausian walnut). The phloem of some thirty species of other lower dicotyledonous trees has also been investigated in a preliminary way. Next year this research will be continued. A general account of the literature on the subject will be presented in the subsequent paper.

The sieve tubes of the gymnosperms and the vascular cryptogams have sieve plates on their lateral walls as well as on their fusiform end walls; while in the angiosperms true and typical sieve plates are supposed to be confined to the oblique or horizontal end walls of the sieve tube. HILL[2] states:

> The term "sieve field," in the sense in which it is used in this paper, denotes the group of fine connecting threads or strings which are found normally on the lateral walls, and which serve as a means of communication between adjoining sieve tubes. The sieve plates occur on the horizontal or oblique end walls of the sieve tubes, and occasionally on the lateral walls also, but their slime strings are readily distinguished from sieve fields owing to their large size.

The object of the present research was to discover, if possible, any ancestral characters of the phloem, and especially to determine if the sieve tubes of any of the lower dicotyledons had lateral "sieve plates" instead of lateral "sieve fields."

In collecting material, it was found that the pieces of tissue from the main trunk of large trees were most satisfactory. Specimens taken from the trunk near the ground were texturally too

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 32.

[2] HILL, T. G., Histology of sieve tubes of the angiosperms. Annals of Botany **22**:265. 1908.

irregular to be used for making radial sections. Phloem from large branches did not show much callus, specimens usually presenting in radial section but two or three rows of sieve tubes with callus.

The material used was cubes about a centimeter each way, which included the cambium as well as the phloem. These were killed, fixed, and softened, and then imbedded in celloidin. For general study the sections were double stained with hematoxylin-safranin and mounted in balsam. Russow's callus reagent was used to demonstrate the callus.

It will be appropriate to consider first the figures which accompany this paper. Figs. 1 and 2 show the topography of the phloem of *Carya alba* under lower power. The sections used for these were stained with hematoxylin-safranin. Fig. 3 is a higher-power magnification of a part of fig. 2. Figs. 4–6 are views of sections of *Carya glabra* that were recently treated with Russow's callus reagent.

Fig. 1 is a radial longitudinal section. At the left side of this section are seen two rows of sieve tubes with portions of end walls showing sieve plates in face view, and along the right side lateral sieve plates are shown in cross-section. The long, narrow, thick-walled cells are bast fibers. These usually occur in groups of three to six as seen in radial view.

The larger phloem parenchyma cells contain prismatic crystals which have elongated, nucleus-like spots in the center. The rays are made up of short parenchyma cells that have several simple pits where they come in contact with phloem parenchyma. A portion of a ray is shown in the left side of this section. No crystals have been observed in the ray parenchyma cells of any of the Juglandaceae studied.

Fig. 2 is a tangential section. Many crystal-bearing phloem parenchyma cells are seen in this view also. The large cells with oblique end walls are sieve tubes. They show the lateral sieve plates very strikingly in face view, and cross-sections of terminal sieve plates on the slanting end walls. This section shows but few bast fibers. The phloem parenchyma cells toward the lower right side of this figure, wherever their starch content is not too dark, may be seen to have densely pitted radial walls. The rays vary from uniseriate to multiseriate.

Fig. 3 is a high-power view of a part of that shown in fig. 2. On the left side there is again a good view of crystal-bearing phloem parenchyma cells. In the center there is a large sieve tube with lateral sieve plates covering the entire tangential wall. These lateral sieve plates when appropriately stained are found to be filled with angular pits with a fine netlike mesh between. They appear to be exactly the same as the terminal sieve plates.

Fig. 4 is a radial section of *Carya glabra*, stained with Russow's callus reagent. At the top and bottom are shown in face view terminal sieve plates covered with callus. Between these two sieve tubes are the dark spots of callus on the lateral sieve plates in cross-section.

Fig. 5 is a view similar to fig. 4. On the right is a portion of a ray showing the parenchyma cells with patches of dark-stained starch grains. On the left is again seen some phloem parenchyma cells containing large crystals.

Fig. 6 shows the center portion of fig. 5 more highly magnified. The dark dashes along the center are cross-sections of the deeply stained lateral callus. The writer has counted 40–50 of these in a straight line along the side of a large sieve tube.

Carya has relatively larger sieve tubes than *Juglans* or *Pterocarya*. In cross-section they are as much larger than the other elements of the tissue as medium sized vessels of the xylem are larger than the tracheids.

The phloem of *Juglans* and *Pterocarya* is much like that of *Carya*, but there are a few general characteristics by which they may be readily separated. The crystal-bearing phloem parenchyma cells of *Juglans cinerea* and *Juglans nigra* are nearly cubical, and each contains a druse, while those of *Carya* are longer than wide and contain prismatic crystals. *Juglans nigra* has very many crystals, especially in specimens from the trunk of large trees. Besides the crystals in the parenchyma, the bast fibers are often filled with rows of cubical crystals. These bast fibers of *Juglans nigra* occur in widely interrupted rings, while in *Juglans cinerea* the rings of bast fibers are nearly continuous. The bast fibers of *Juglans* and *Pterocarya* are thick-walled and keep a more or less circular outline; while *Carya* has relatively much more numerous

elements of the hard bast, yet as these are thinner-walled they tend to collapse and show an irregular outline in cross-sections.

The expanded ends of the large rays of *Juglans cinerea* are noticeable in rather thin specimens of phloem from young trees or small branches, but are seen in only rather thick phloem of *Juglans nigra*. The large sieve tubes of *Juglans nigra* and *Juglans cinerea* have long, crowded, lateral sieve plates like those shown in fig. 3 for *Carya*, but the smaller sieve tubes have sieve plates that are farther apart and have an oval or circular outline.

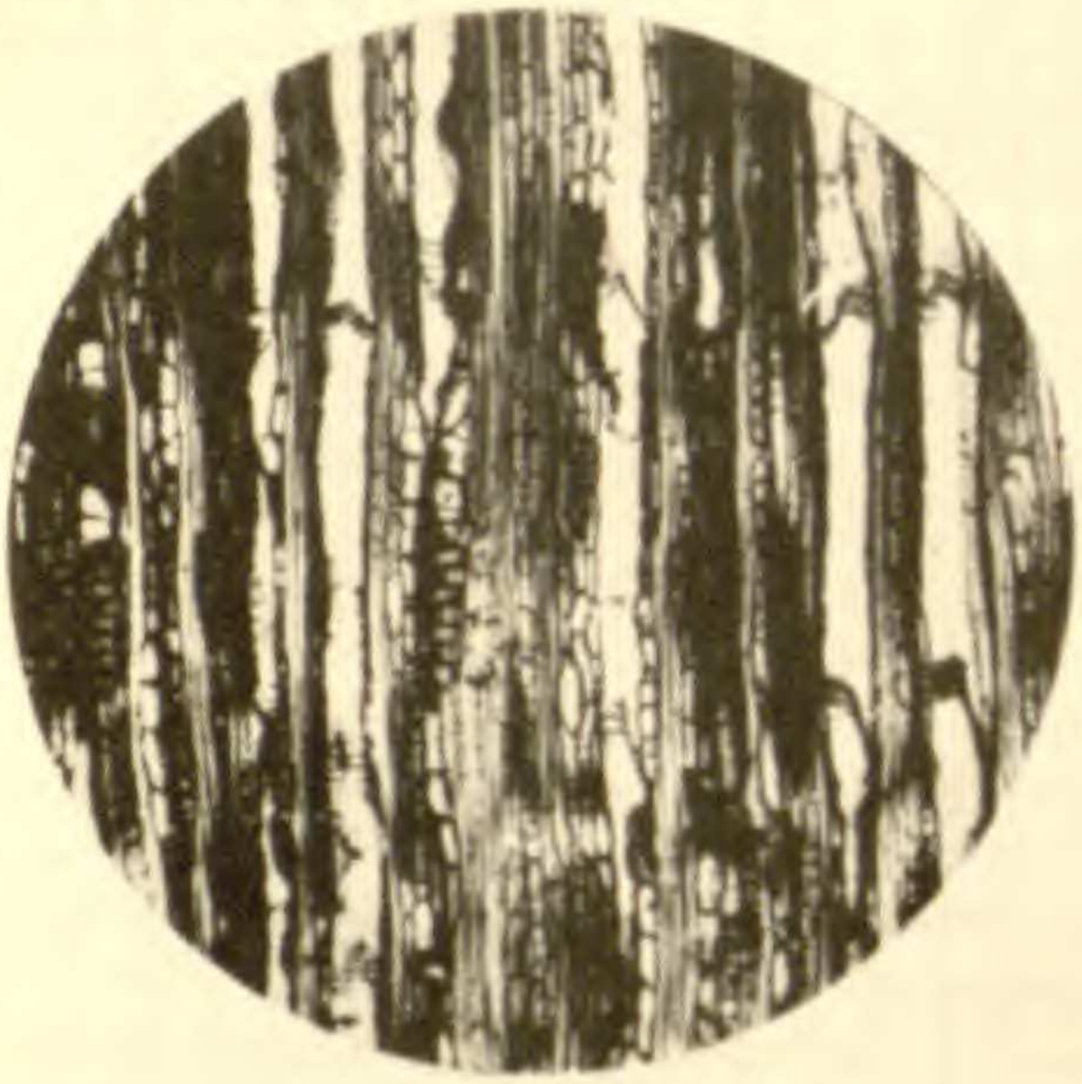
There are no crystals in the phloem of *Pterocarya* except druses in the parenchyma of root phloem. The phloem of *Pterocarya* has nearly continuous bands of bast fibers alternating with wider bands of sieve tubes and bast parenchyma. The lateral sieve plates in *Pterocarya* are practically the same as in *Juglans*, except that in the larger sieve tubes some of the longer sieve plates are divided obliquely by thin bars. The lateral sieve plates of *Juglans* and *Pterocarya* show equally as well developed callus as *Carya glabra*, though the sieve tubes do not appear to function as long. In some specimens taken from branches of *Pterocarya* and *Juglans*, callus was evident only on the fifth or sixth row of sieve tubes from the cambium. While in similar specimens of *Carya*, callus was present farther from the cambium and was on several rows of sieve tubes.

Where sieve plates occur on the side of a sieve tube next the companion cell, unilateral callus was observed. This callus resembles the unilateral callus described by STRASBURGER[3] on the sieve plates of sieve tubes of Abietineae next to the marginal ray cells.

Lateral callus is plentiful in the sieve tubes of *Castanea*, *Salix fragilis*, and *Populus trichocarpa*, though usually not so thick as on the end walls.

A sort of tyloses occurs occasionally in the older sieve tubes of the Juglandaceae. It is formed not by the wall of a parenchyma cell pushing in through a pit, as in the vessels of the xylem, but by a portion of the sieve tube wall subtending a parenchyma cell growing bodily into the sieve tube. The tyloses of the sieve tubes

[3] STRASBURGER, ED., Histologische Beiträge **3**:1891.



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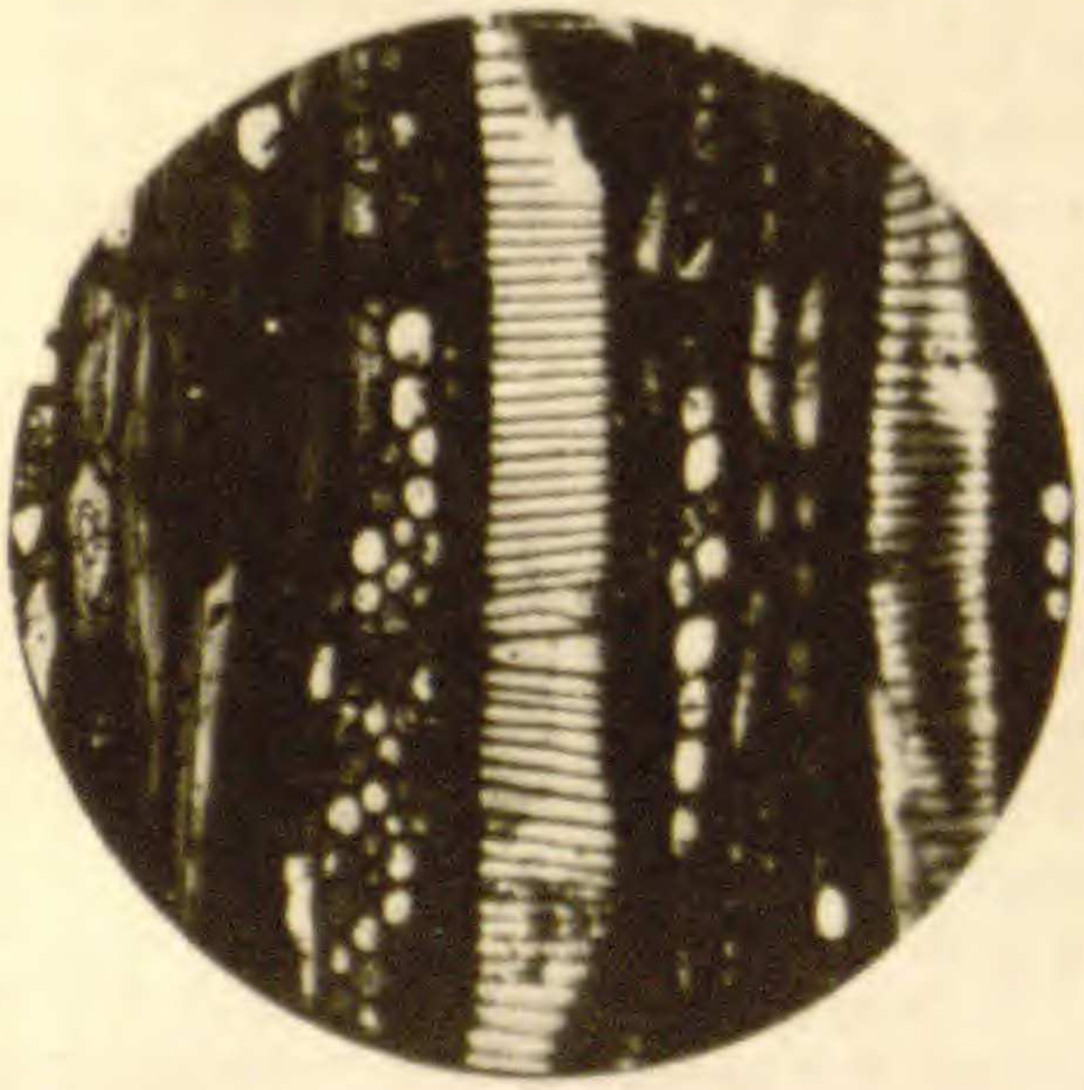

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